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Research Article

How wintering waterbird communities assemble and respond to environmental variation in satellite wetlands around Chao Lake, China

Mingyun Yuan[1], Guangyao Wang[2], Zhiru Lu[1], Chunlin Li[1,3], Willem F. de Boer[4]

1 *School of Resources and Environmental Engineering, Anhui University, Hefei, 230601, China*
2 *School of Geography and Planning, Chizhou University, Chizhou, 247000, China*
3 *Anhui Province Key Laboratory of Wetland Ecosystem Protection and Restoration, Anhui University, Hefei, 230601, China*
4 *Wildlife Ecology and Conservation Group, Wageningen University & Research, 6708PB, Wageningen, Netherlands*

Corresponding author: Chunlin Li (lichunlin1985@163.com)

Abstract

Waterbirds are increasingly reliant on smaller, spatially separated but ecologically connected satellite wetlands amid the global loss and degradation of large natural wetlands. However, how waterbirds use these wetlands remains poorly understood. Between November 2023 and February 2024, we conducted four monthly surveys of wintering waterbirds across 55 satellite wetlands surrounding Chao Lake, a typical river-connected lake in the middle and lower reaches of the Yangtze River that is now hydrologically disconnected from the main river. We quantified taxonomic (species richness and Shannon diversity), functional and phylogenetic mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), examined their temporal dynamics and environmental drivers, and compared functional, and phylogenetic indices with null models to test the assembly process. We recorded 20,425 individuals of 44 species, averaging 31 species per month, with noticeable temporal variation. Species richness was lowest in November and did not differ among other months; Shannon diversity was lower in November than in December but otherwise similar, while functional and phylogenetic diversity remained stable over time. Species richness increased with wetland area, habitat diversity, landscape connectivity, and distance from settlements, but decreased with shape complexity, while the Shannon index was positively associated with habitat diversity and distance from roads. Functional and phylogenetic clustering increased with greater landscape connectivity. Both dimensions became more over-dispersed with increasing shape complexity, while greater distance from settlements enhanced functional overdispersion but promoted phylogenetic clustering. Phylogenetic MPD was not significantly associated with any environmental variable. Functional and phylogenetic MPD and MNTD matched null expectations, indicating that stochastic processes dominated wintering waterbird community assembly in these wetlands. This study enhances understanding of community assembly in fragmented wetlands and offers insights for their conservation and management.

Key words: Functional diversity, phylogenetic diversity, stochastic processes, taxonomic diversity, wetland degradation

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Introduction

Large natural wetlands play an important role for waterbirds by providing the habitats necessary for feeding, breeding, and overall survival (VonBank et al. 2022; Gao et al. 2023). However, in recent decades, with agricultural expansion, urbanization, pollution, and other human activities, large wetlands have been confronted with reductions in area, hydrological alteration, and the degradation of ecological functions, among other problems (Fluet-Chouinard et al. 2023). These changes have diminished food resources for waterbirds and intensified competition among them (Finlayson et al. 2024). Consequently, many waterbird species have experienced population declines and contractions in their distribution ranges (Amano et al. 2020).

Against this backdrop, global studies have shown that many waterbirds increasingly rely on satellite wetlands surrounding large wetlands (Donnelly et al. 2022; Paulino et al. 2025; Wang et al. 2025). These satellite wetlands are shaped by both natural hydrological processes and human activities, including mudflats, shallow ponds, vegetated depressions, aquaculture ponds, and seasonally flooded farmlands (Cantonati et al. 2020). They are spatially separated from each other and from large wetlands, yet remain connected through various ecological processes (Wang et al. 2025). Satellite wetlands are smaller, more fragmented, and more susceptible to human disturbance and other threats, and are characterized by greater variability in hydrology and habitat factors (Keinath et al. 2017). Nevertheless, because they are often numerous and occur in high densities, the combination of multiple satellite wetlands can collectively provide diverse microhabitats and foraging opportunities, thereby attracting waterbirds with different ecological requirements (Cerda-Peña and Rau 2023).

Satellite wetlands, despite their distinct structural and functional features, have received far less research attention than large natural wetlands. Waterbird communities in these systems are influenced by multiple environmental factors and potential threats, which together determine species abundance and distribution, and further shape community functional and phylogenetic structure (Ferrarini et al. 2023). However, most previous studies have focused primarily on taxonomic diversity, overlooking functional and phylogenetic dimensions. As a result, our understanding of how waterbirds in satellite wetlands respond to environmental variation and the mechanisms driving their community assembly remains limited. Functional diversity reflects variation in ecological roles such as diet, foraging strategy, and habitat use, whereas phylogenetic diversity represents evolutionary relatedness that constrains species' ecological responses along environmental gradients (Spasojevic and Suding 2012). Integrating taxonomic, functional, and phylogenetic perspectives provides a more comprehensive framework for assessing community assembly and environmental responses in satellite wetlands (Montaño-Centellas et al. 2020).

The middle and lower reaches of the Yangtze River, characterized by numerous river-connected lakes, have long served as crucial wintering areas for migratory waterbirds along the East Asian–Australasian Flyway (He et al. 2022). Historically, these lakes exhibited natural hydrological fluctuations, creating diverse habitats such as shallow zones, mudflats, and vegetated margins that provided abundant foraging and roosting opportunities for waterbirds during winter (Li et al. 2024). In recent decades, however, the construction of sluices and embank-

ments has disrupted the hydrological connectivity between many lakes and the Yangtze River (Xia et al. 2020). Year-round high water levels have hindered natural drawdown, reduced habitat heterogeneity, and further aggravated wetland degradation, leaving many waterbirds unable to find suitable foraging and resting habitats within the main lakes (Liang et al. 2022). Under these circumstances, a large number of waterbirds have been observed in surrounding satellite wetlands, which now serve as important alternative habitats (Liu et al. 2020). However, how these waterbirds utilize these wetlands, respond to environmental factors, and assemble their communities remains poorly understood.

In this study, we conducted four monthly surveys of wintering waterbirds between November 2023 and February 2024 in 55 satellite wetlands surrounding Chao Lake, a typical river-connected lake in the middle and lower reaches of the Yangtze River that has long been hydrologically disconnected from the main river. We quantified taxonomic (species richness and Shannon diversity), functional and phylogenetic mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), examined their temporal dynamics and environmental drivers, and compared functional and phylogenetic indices with null models to test the assembly process. We hypothesized that greater habitat diversity, larger wetland area, and stronger connectivity would support higher species richness and Shannon–Wiener diversity by increasing ecological niches, resources, and dispersal opportunities (Masto et al. 2024). We also expected that wetlands with more irregular shorelines would show greater functional and phylogenetic differentiation, as complex edges create diverse microhabitats for species with different ecological and evolutionary traits (Matuoka et al. 2020). Finally, we predicted that stochastic processes would dominate, as the small spatial scale limits the strength of environmental filtering (Daniel et al. 2019). By analysing these relationships, we aim to improve understanding of how wintering waterbirds respond to environmental factors across satellite wetlands and to inform their conservation and management.

Methods

Study area

Chao Lake (31°25'–31°43'N, 117°16'–117°51'E) is located in the middle and lower reaches of the Yangtze River in China (Fig. 1). The basin is flat and experiences a subtropical monsoon climate, with mean annual precipitation of about 1,000 mm, mostly from June to September. Since the 1950s, sluices such as Yuxi and Chao Lake have disconnected the lake from the Yangtze River (Hou et al. 2024). Numerous satellite wetlands occur along the lake margins, mainly in the northern, eastern, and southwestern sectors, often near inflow rivers, villages, or agricultural areas in low-lying, poorly drained terrain. The main satellite wetland types include aquaculture ponds, paddy fields, reservoirs, and natural ponds. Aquaculture ponds (0.1–50 ha) are usually arranged in contiguous patches, sometimes forming complexes exceeding 100 ha. They are enclosed by low earthen dikes, maintain water depths of 80–150 cm during cultivation, and are typically drained in winter, exposing mudflats for several weeks (Li et al. 2015). Paddy fields follow a double-cropping system with rice harvested in July and October, after which most are planted with winter crops or left fallow

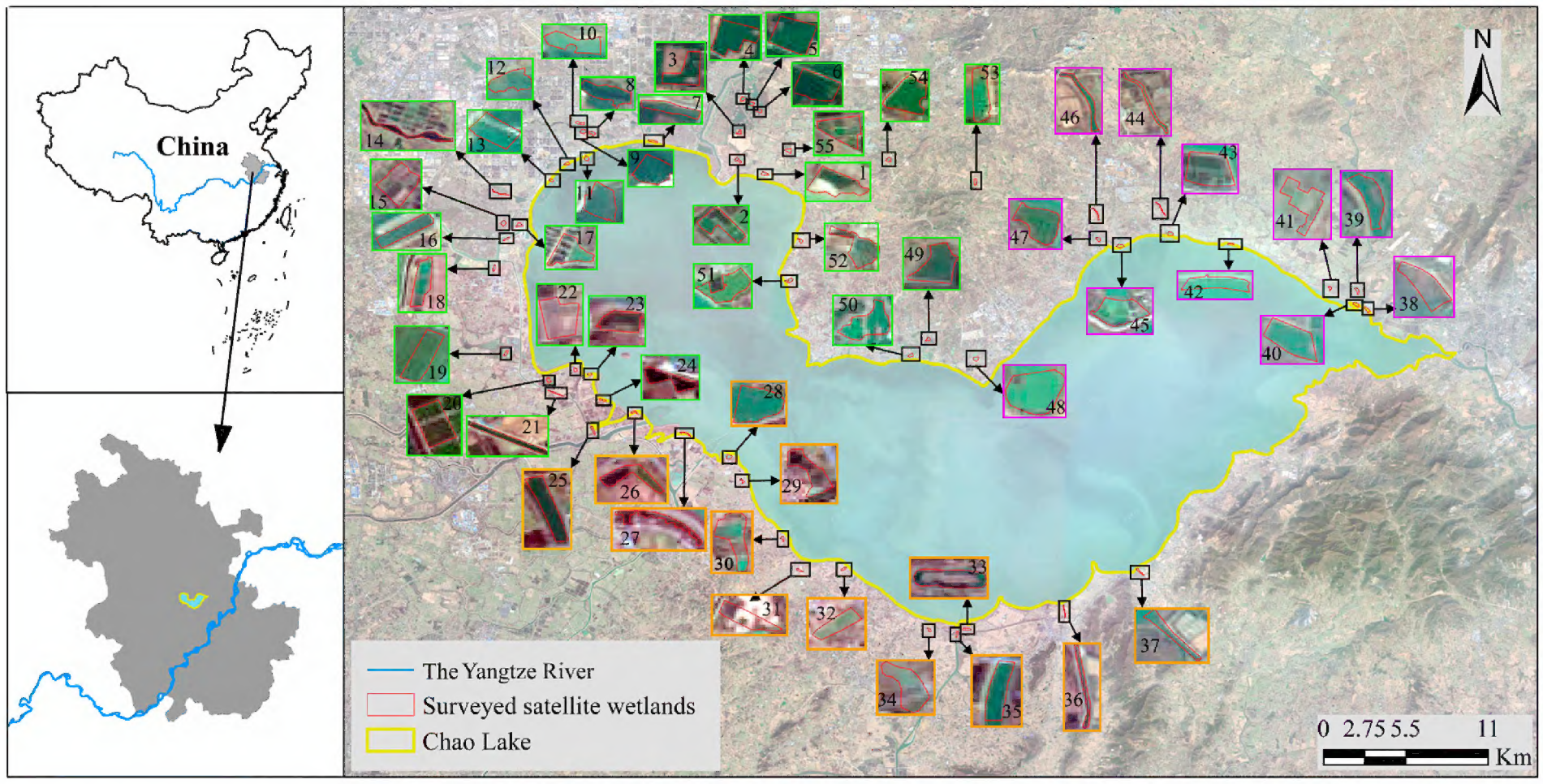

Figure 1. Field survey sites of satellite wetlands surrounding Chao Lake in eastern China. The numbers (1–55) indicate the unique identifiers of the surveyed wetlands. The inset maps show the detailed boundaries of each wetland site. The coloured borders of the inset maps indicate the three primary spatial sub-regions: green for the northwestern cluster (n = 31), purple for the northeastern cluster (n = 11), and orange for the southern cluster (n = 13).

with shallow water. Reservoirs are generally small and regular in shape with managed water levels, whereas natural ponds are irregular, less controlled, and often covered by aquatic vegetation.

Potential satellite wetlands were first identified using Google Earth, followed by ground surveys to verify their accessibility and suitability for field observation. To ensure a random sampling design, we established a pool of candidate wetlands and used a random number generator to select 55 sites for the survey, with areas ranging from 2.5–7.56 ha and exhibiting varied shapes, sizes, and environmental attributes. All sites were located within 10 km of the main body of Chao Lake. Spatially, these wetlands exhibited a clustered distribution, forming three primary sub-regions: a northwestern cluster (n = 31), a northeastern cluster (n = 11), and a southern cluster (n = 13) (Fig. 1). Across the entire network, the average nearest-neighbour distance was 1.80 ± 1.26 km. These sites were representative of the general characteristics of satellite wetlands surrounding Chao Lake.

Waterbird survey

Surveys were conducted from November 2023 to February 2024, once in the middle of each month, using the point count method (Bibby et al. 2000). Each survey round lasted three consecutive days and was conducted under clear, windless conditions. To minimize observer bias, the same single survey team conducted all counts across all sites. At each satellite wetland, one to three observation points were set according to its area, shape, and surrounding environment to ensure full site coverage (Si et al. 2018). Each observation point was surveyed for 20 minutes. Binoculars (10×42 WB Swarovski) and a spotting scope (20–60×

Swarovski ATM 80) were used for all surveys. Following the Ramsar Convention, waterbirds were defined as species ecologically dependent on wetlands. At each point, we recorded all waterbird species and their abundances using the sampled wetlands, excluding individuals merely flying over (Delany 2005). To minimize observer bias, the same survey team conducted all counts.

Environmental variables

We quantified seven environmental variables for each satellite wetland and divided them into three groups: anthropogenic, local attributes, and connectivity (Table 1; Wang et al. 2025). All environmental variables were measured once during the period from the first survey to December 15, 2023. Given that these variables are primarily static landscape metrics (e.g., area, distance) or relatively stable habitat features during the non-growing winter season, the measured values were representative of the environmental conditions throughout the four-month survey period.

Wetland area, perimeter, the shortest distance to the nearest major settlement (area >10 hectares), the shortest distance to the nearest major road, and the nearest-neighbour distance between surveyed sites were calculated using field surveys and high-resolution Google Earth maps. To characterize the spatial arrangement, we used K-means clustering analysis to identify spatial sub-regions. The shape index was calculated based on the method of Patton (1975). We extracted, for each satellite wetland, the total area of wetlands within a 3-km radius from the cloud-free Sentinel-2B (L2A-level) land-cover map and

Table 1. Measured habitat variables of satellite wetlands around Chao Lake (mean ± SE, and range), along with their corresponding descriptions and expected effects.

Variables	Description	Mean ± SE (Range)	Expected effect
Local attributes			
AW (ha)	Area of each wetland	5.06 ± 0.20 (2.53–7.56)	+
PW (km)	Perimeter of each wetland	1.18 ± 0.05 (0.71–2.35)	+ / 0
HD	Habitat diversity within each wetland	1.69 ± 0.04 (1.13–2.35)	+
SI	Each wetland's shape index: (L, A is wetland perimeter and area, separately)	1.51 ± 0.07 (1.06–3.14)	–
Anthropogenic			
SS (km)	Shortest distance between each wetland and nearest main human settlement (>10 ha)	0.85 ± 0.11 (0.01–3.04)	+
DR (km)	Shortest distance between each wetland and nearest main road	0.71 ± 0.16 (0.01–5.22)	+
Landscape Connectivity			
LC (ha)	Total area of wetlands (>1 ha) within a 3 km buffer zone surrounding each wetland	1782.15 ± 99.89 (923.24–3200.45)	+

Note: Expected effects indicate the hypothesized relationships between each variable and species richness based on Masto et al. (2024) and Matuoka et al. (2020). "+" represents a positive effect, "–" a negative effect, and "+/0" an uncertain or context-dependent effect.

used this value (excluding the focal wetland itself) as the quantitative measure of its landscape connectivity (Salgueiro et al. 2021). The image was acquired on January 15, 2024, and downloaded from the European Space Agency Copernicus Open Access Center. The land cover map was generated using the support vector machine classification tool in ENVI 5.3 (Exelis VIS, Inc.), and six land cover types were identified: built-up area, mudflat, open water, aquatic vegetation, woodland, and farmland. Habitat diversity (HD) was calculated using the Hill Shannon-Wiener index within the counting area of each satellite wetland (Hill 1973; Eq 1):

$$HD = -\sum_{i=1}^{n} p_i \log p_i \quad \text{(Eq 1)}$$

where P_i represents the proportion of the *i*-th habitat type among the *n* types within the observation area of each satellite.

Functional traits and phylogenetic data

Functional diversity may depend on arbitrary decisions regarding trait selection, and there is no consensus on which species characteristics best capture species' functional roles. To ensure comparability across studies, a consistent set of traits is recommended (Petchey and Gaston 2006). We followed Li et al. (2019) to select four traits to measure the functional diversity of waterbird assemblages, comprising one continuous and three categorical attributes (Table 2). Body mass, related to species' resource requirements, was treated as a continuous trait and represented the mean value for each species obtained from published literature. The categorical traits—namely primary diet (3 categories), foraging method (6 categories), and foraging stratum (3 categories)—were considered binary traits (0 or 1). Each species was assigned to a single category within each trait type, based on its predominant diet or foraging behaviour described in published sources. When potential overlaps occurred, the dominant trait was used for classification. Phylogenetic signals for functional traits were calculated using Blomberg's K to assess the degree of phylogenetic conservatism (Blomberg et al. 2003). Body mass data were obtained from Wang et al. (2021), while diet and foraging stratum data were sourced from Wilman et al. (2014).

Before calculating the functional diversity of waterbird communities, we first calculated functional dissimilarity between all species pairs using the Gower distance, which accommodates mixed data types (Botta-Dukát 2005). Then, we constructed a functional dendrogram of community species using the unweighted pair group method with arithmetic mean (UPGMA)(Swenson 2014).

For phylogenetic data, we used the global bird phylogeny database (http://birdtree.org), and selected the "Hackett All Species: a set of 10,000 trees with 9,993 OTUs each" option in the "Phylogeny subsets" tool to build a phylogenetic tree containing all species recorded in the field survey. First, we generated 5,000 phylogenetic trees from the pseudo-posterior distribution. Then, using the "BEAST2" package in TreeAnnotator (version 2.6.3), we selected the "mean node heights" method to obtain the maximum clade credibility tree (Rubolini et al. 2015). The final phylogenetic tree was visualized and edited using Figtree v1.4.3 (http://tree.bio.ed.ac.uk/), and used for all subsequent phylogenetic analyses (Bouckaert et al. 2014).

Table 2. The functional traits used to calculate the functional diversity of bird assemblages and their phylogenetic signals (Blomberg's K).

Functional Traits	Trait Types	Value Type	*K*	*p*
Body mass	Body mass (g)	Continuous	0.483	**0.009**
Primary diet	Invertebrates	Binary	0.079	0.643
	Vertebrates	Binary	0.011	0.758
	Plants	Binary	0.544	**0.001**
Foraging method	Pursuit	Binary	0.139	0.413
	Gleaning	Binary	0.191	0.076
	Pouncing	Binary	1.429	**0.001**
	Grazing	Binary	0.123	0.302
	Digging	Binary	0.200	0.313
	Probing	Binary	0.286	**0.024**
Foraging stratum	Water	Binary	0.218	0.518
	Mud	Binary	0.012	0.517
	Vegetation	Binary	0.005	0.902

Notes: A higher K index value indicates a stronger phylogenetic signal. P-value indicate the significance of the phylogenetic signal for the functional trait, with values below 0.05 shown in bold.

Diversity indices

To characterize the multidimensional structure of waterbird communities, we calculated taxonomic, functional, and phylogenetic diversity for each wetland in each survey.

Taxonomic diversity was quantified using species richness (SR, i.e. the total number of species) and the Shannon-Wiener diversity index (H'; Eq 2), as:

$$H' = -\sum_{i=1}^{n} p_i \log p_i \quad \text{(Eq 2)}$$

where P_i is the proportion of individuals of the *i*-th species relative to the total number of individuals.

Functional diversity (FD) and phylogenetic diversity (PD) were assessed using a trait-based dendrogram and a phylogenetic tree constructed from species-level ecological traits and established avian phylogenies. For each community, we computed two abundance-weighted metrics for both FD and PD: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). MPD reflects the average distance among all species pairs, representing overall functional or phylogenetic divergence. MNTD measures the average distance to the nearest neighbour, capturing the degree of terminal clustering in trait or evolutionary space (Webb 2000).

Data analysis

We used generalized linear mixed models (GLMMs) to test the effects of environmental variables on taxonomic, functional, and phylogenetic diversity indices (Bolker et al. 2009). Each diversity index was modelled as a response

variable under a Gaussian error distribution. Prior to analysis, all continuous environmental variables were standardized using z-scores (La Sorte et al. 2018). Multicollinearity was assessed via variance inflation factors (VIF), and variables with VIF > 10 were excluded (only wetland perimeter had VIF > 10) (Naimi et al. 2014). Wetland identity and survey month were included as random effects. Model selection was conducted by backward elimination of non-significant predictors. We used Moran's I statistic to examine spatial autocorrelations (Ehbrecht et al. 2021), but without significant results ($p \geq 0.05$ in all models). All statistical analyses were performed using R version 4.3.3, with p-values ≤ 0.05 considered statistically significant (R Core Team 2023).

Null model and assembly process

To infer the ecological processes shaping community assembly, we applied null models to test whether observed functional and phylogenetic diversity deviated from random expectations. For each wetland and survey round, 999 randomized communities were generated by reshuffling species identities while maintaining observed species richness and occurrence frequencies across the regional pool. Mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) were then calculated for each randomized community using the same trait matrix and phylogenetic tree as the observed data. The standardized effect size (SES; Eq 3) was computed as:

$$\mathrm{SES} = \left(\mathrm{M}_{\mathrm{null}} - \mathrm{M}_{\mathrm{obs}}\right) / \mathrm{SD}_{\mathrm{null}} \quad \text{(Eq 3)}$$

where M_{null} and M_{obs} represent the mean MPD or MNTD from simulated and observed communities, respectively. The standardized MPD and MNTD correspond to the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI), quantifying overall and terminal clustering or overdispersion. NRI or NTI values greater than +1.96 indicate clustering driven by environmental filtering, whereas values below −1.96 suggest overdispersion due to limiting similarity or competition. Values between −1.96 and +1.96 were considered random, implying stochastic assembly processes (Webb et al. 2006).

Results

Waterbird community composition

Across four monthly surveys rounds of 55 satellite wetlands around Chao Lake, we recorded 20,425 individual waterbirds belonging to 44 species. There were 27 species in November, 29 in December, 33 in January, and 33 in February, averaging about 31 per month. Among them, six were nationally protected in China, including two Class I species, Baer's Pochard (*Aythya baeri*) and Oriental Stork (*Ciconia boyciana*), and four Class II species. In addition, seven species were listed in the IUCN Red List, ranging from Near Threatened (NT) to Critically Endangered (CR). Baer's Pochard, Oriental Stork, and Eurasian Curlew (*Numenius arquata*) were included in both national and international protection lists (Table 3).

Table 3. Nationally Protected and Threatened Waterbird Species Recorded in Satellite Wetlands around Chao Lake (November 2023–February 2024).

Common Name	Scientific Name	National Protection Status (China)	IUCN Red List Status
Baer's Pochard	*Aythya baeri*	Class I	CR
Oriental Stork	*Ciconia boyciana*	Class I	EN
Tundra Swan	*Cygnus columbianus*	Class II	–
Smew	*Mergellus albellus*	Class II	–
Eurasian Spoonbill	*Platalea leucorodia*	Class II	–
Eurasian Curlew	*Numenius arquata*	Class II	NT
Common Pochard	*Aythya ferina*	–	VU
Northern Lapwing	*Vanellus vanellus*	–	NT
Ferruginous Duck	*Aythya nyroca*	–	NT
Falcated Duck	*Anas falcata*	–	NT

Note: CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened.

Temporal dynamics of multidimensional diversity

Species richness (SR) was lowest in November ($F_{3,162}$ = 9.23, $p < 0.001$), with no significant differences among other months. Shannon-Wiener diversity index (H') was lower in November than in December ($F_{3,162}$ = 2.68, $p = 0.049$), while also no significant differences were detected among other months. Also, phylogenetic and functional diversity indices (MPD and MNTD) showed no significant differences among the four months (Phylogenetic MPD: $F_{3,162}$ = 1.23, $p = 0.299$; Phylogenetic MNTD: $F_{3,162}$ = 1.73, $p = 0.164$; Functional MPD: $F_{3,162}$ = 2.03, $p = 0.112$; Functional MNTD: $F_{3,162}$ = 0.16, $p = 0.925$; Fig. 2).

Effects of environmental factors on diversity metrics

As expected, habitat diversity (HD) had a positive effect on both species' richness and Shannon diversity in wetlands (Fig. 3). With increasing distance to major settlements (i.e. SS) species richness and functional MPD also increased, but phylogenetic MNTD decreased. The wetland shape index (SI) was negatively correlated with only species richness, while showing positive effects on phylogenetic MNTD, functional MPD, and functional MNTD. Landscape connectivity (LC) positively affected species richness, but was negatively associated with both phylogenetic MNTD and functional MNTD. In addition, wetland area (AW) had a positive effect on species richness, and distance to major roads (DR) had a positive effect on Shannon diversity. Notably, phylogenetic MPD showed no significant association with any environmental variable (Fig. 3).

Community assembly

Across the four months, phylogenetic and functional NRI and NTI values mostly fell within the –-1.96 to +1.96 range, with few sites exceeding these thresholds. This pattern indicates that community assembly of wintering waterbirds in satellite wetlands was largely governed by random processes and remained relatively stable across the four months. (Fig. 4).

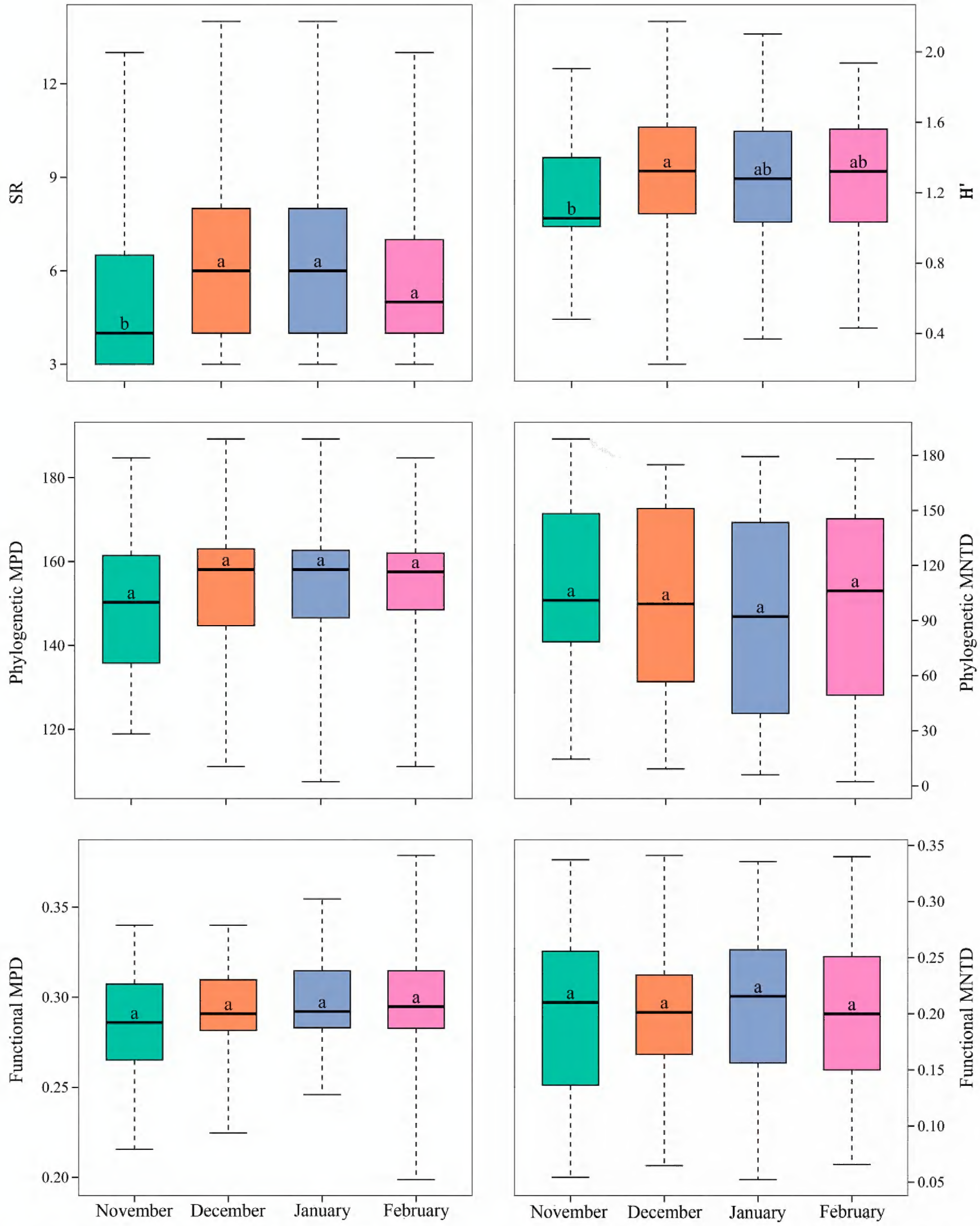

Figure 2. Monthly variation in multiple biodiversity indices of wintering waterbird communities in satellite wetlands around Chao Lake. Boxplots sharing the same letter indicate no significant difference based on repeated-measures ANOVA followed by Tukey's post hoc test. MPD: the mean pairwise distance; MNTD: the mean nearest taxon distance; SR: species richness; H': Shannon-Wiener diversity index.

Discussion

From November 2023 to February 2024, we recorded a large number of species and individual waterbirds across satellite wetlands. This high abundance and diversity indicate that these sites serve as critical foraging and resting habi-

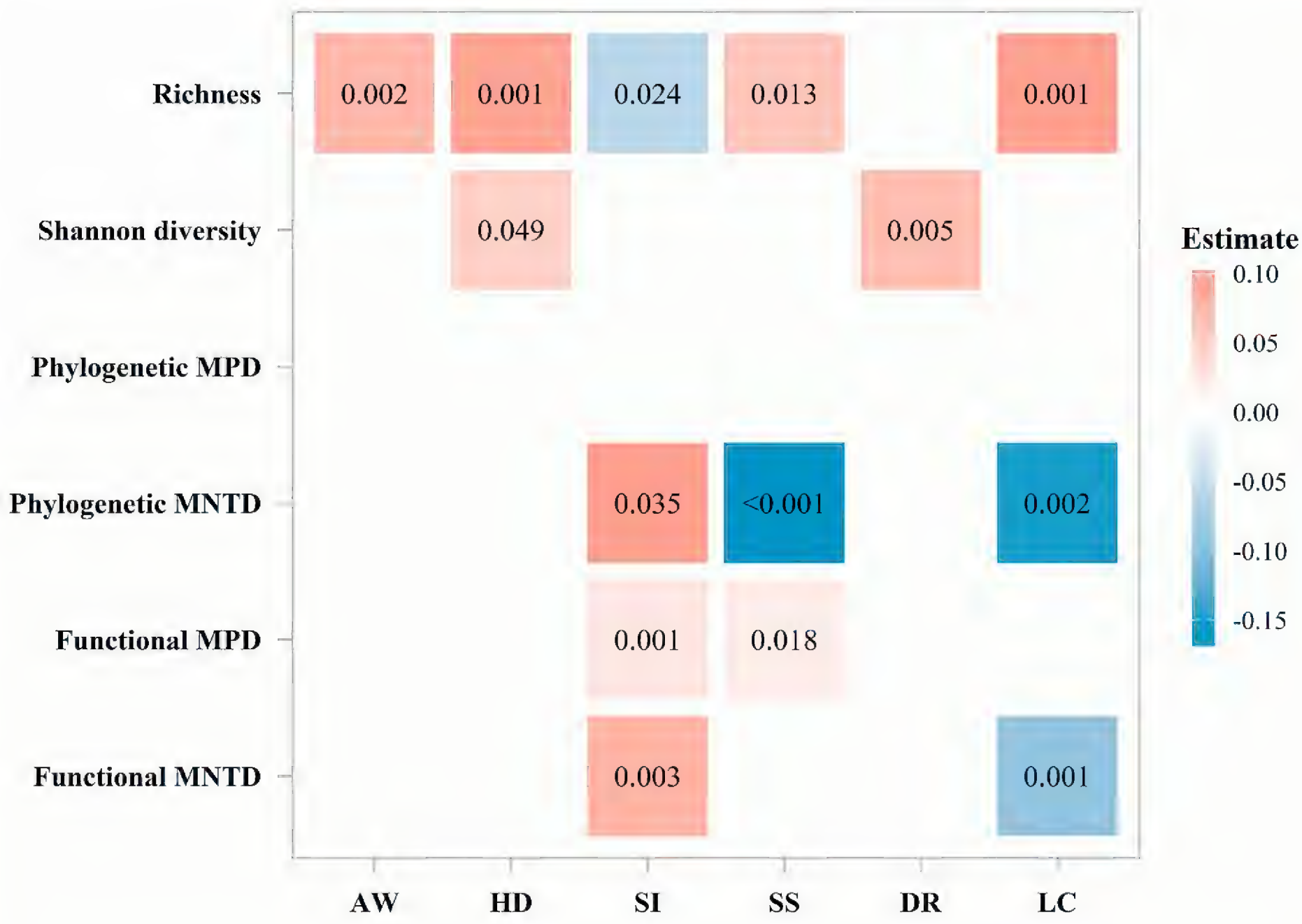

Figure 3. Heatmap showing significant relationships ($p \leq 0.05$) between diversity metrics and environmental factors. Colors indicate the direction and strength of regression coefficients (red, positive; blue, negative). Numbers denote p-values, with $p < 0.001$ shown as "< 0.001". AW: area of each wetland; HD: habitat diversity; SI: shape index; SS: distance to nearest settlement; DR: distance to nearest road; LC: landscape connectivity; MPD: mean pairwise distance; MNTD: mean nearest taxon distance.

tats for maintaining regional waterbird diversity (Wang et al. 2025). This may be because the environmental degradation of large wetlands has increased the difficulty for waterbirds to access sufficient food resources, forcing them to rely more heavily on nearby satellite wetlands (Laursen et al. 2025). Moreover, waterbird communities in satellite wetlands exhibited temporal dynamics. In November, both species richness and Shannon-Wiener diversity were markedly lower, which may reflect the early stage of community assembly during the wintering period. At this time, only a limited number of migratory species had arrived, mainly those with an earlier migration or lower cold tolerance (Lorenzón et al. 2020). As more individuals gradually reached the area, community composition became richer and more taxonomically diverse (Che et al. 2019). In contrast, functional and phylogenetic diversity remained stable, likely because newly arriving species shared similar traits and evolutionary histories with those already present (Ricotta et al. 2020). Trait redundancy and phylogenetic conservatism in the wintering waterbird assemblages may have constrained variation in these dimensions, even as species richness increased (Cooke et al. 2019).

We found that both species richness and Shannon–Wiener diversity were higher in wetlands with greater habitat diversity likely because diverse habitat types provide complementary resources for different ecological groups

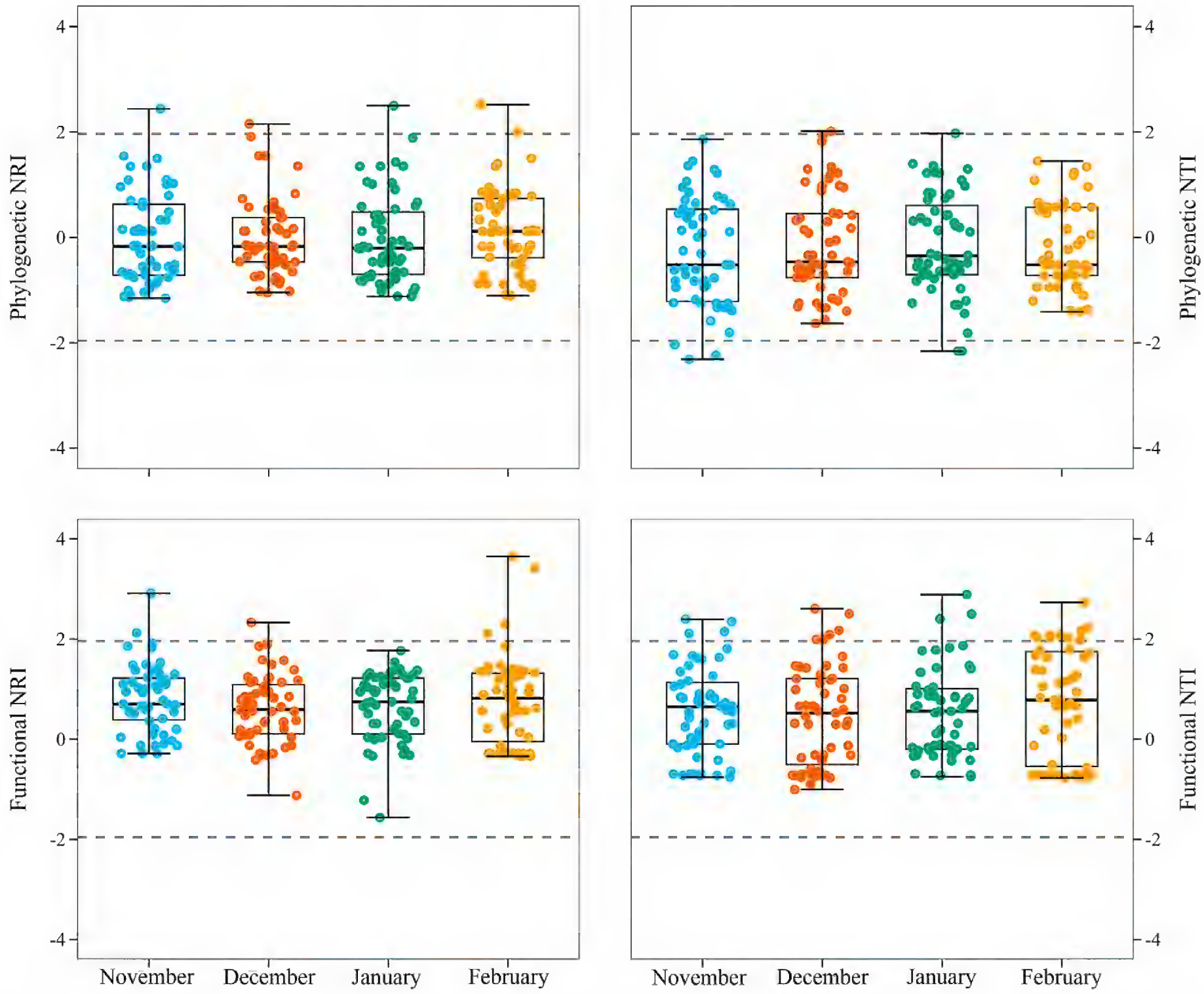

Figure 4. Monthly variations in community assembly indices of waterbird communities in satellite wetlands around Chao Lake. The dashed lines represent the significance thresholds of +1.96 and −1.96; values > 1.96 indicate significant clustering, values < -1.96 indicate significant overdispersion, and values between -1.96 and 1.96 indicate random community structure. NRI: Net Relatedness Index (standardized MPD, reflecting overall structure); NTI: Nearest Taxon Index (standardized MNTD, reflecting terminal structure).

(Cerda-Peña and Rau 2023). For example, open water supports swimming birds, mudflats attract waders, paddy fields supply feeding grounds for herbivorous species, and aquatic vegetation offers shelter and food for omnivorous waterbirds (Chatterjee et al. 2020). The coexistence of these habitats expands niche space and prevents a few generalist species from dominating, leading to a more balanced community structure (Henry and Cumming 2017). As expected, wetlands with larger areas and stronger connectivity also supported higher species richness, as larger habitats sustain greater resource capacity, and connectivity facilitates waterbird movement and site use across the wetland network (Masto et al. 2024). Furthermore, species richness increased with distance from settlements, and Shannon–Wiener diversity was higher in wetlands farther from roads, suggesting that reduced human disturbance may provide quieter and more stable habitats, alleviating behavioural stress in sensitive species and allowing a wider range of waterbirds to coexist (Lacko et al. 2018). In contrast, wetlands with more irregular shapes had lower species richness,

probably because increased edge effects and reduced core areas limit habitat stability for species requiring continuous environments (Gao et al. 2021).

Interestingly, we observed a trade-off driven by edge effects: while irregular wetland shapes were associated with lower species richness (as noted above), they supported higher functional MPD, functional MNTD, and phylogenetic MNTD. This is likely because irregular shapes facilitate the formation of heterogeneous microhabitats (Xia et al. 2025). For example, complex boundaries typically exhibit higher variability in water depth and vegetation types, creating distinct niches that enable the coexistence of diverse evolutionary lineages and functional guilds (Paulino et al. 2025). This effectively prevents the dominance of similar species, thereby minimizing redundancy and maintaining high diversity in both traits and lineages (Matuoka et al. 2020). Wetlands with higher connectivity exhibited lower functional and phylogenetic MNTD, reflecting greater community similarity likely driven by frequent movements of waterbirds among sites and homogenized resource configurations across connected wetlands (Dias et al. 2020). In our field surveys, generalist dabbling ducks such as *Anas poecilorhyncha* and *Anas platyrhynchos* were frequently recorded across highly connected sites, indicating functional and phylogenetic convergence. In contrast, wetlands farther from settlements had higher functional MPD but lower phylogenetic MNTD, implying that low-disturbance environments promote functional diversification while maintaining phylogenetic clustering (Li et al. 2019). In these wetlands, we observed that species with different foraging strategies, such as *Phalacrocorax carbo*, *Anas strepera*, and *Fulica atra*, often co-occurred, whereas closely related anatids including *Anas strepera*, *Mareca penelope*, and *Anas platyrhynchos* remained dominant, leading to clustering among related taxa. Phylogenetic MPD showed no significant environmental associations, likely because most waterbirds belong to a few closely related lineages, making this broad-scale index less responsive to habitat variation (Montaño-Centellas et al. 2021).

We found that throughout the wintering season, the assembly of waterbird communities in satellite wetlands was predominantly driven by stochastic processes. This pattern may, in part, result from the limited spatial extent of the Chao Lake system, as the relatively small geographic scale constrains environmental variation and thereby weakens deterministic filtering across sites (Daniel et al. 2019). In addition, waterbird behaviour may also play an important role in shaping this pattern. During the wintering period, most waterbirds forage opportunistically and move frequently among wetlands rather than remaining in fixed locations, which disrupts the establishment of stable species–environment relationships and prevents long-term environmental filtering from operating effectively (Ferrarini et al. 2023). Furthermore, their strong mobility, together with the short distances between satellite wetlands, facilitates frequent dispersal and temporary occupancy, enhancing the role of stochastic dispersal limitation and priority effects in determining community composition while reducing the influence of competitive exclusion (Wang et al. 2025).

Conclusion

From November 2023 to February 2024, we found that satellite wetlands around Chao Lake served as important complementary habitats for wintering waterbirds. As expected, wetlands with larger areas and richer habitat compo-

sition supported greater species richness, while the Shannon–Wiener index increased with habitat diversity. In more connected wetlands, species richness was also higher, whereas functional and phylogenetic MNTD values were lower. Wetlands with more irregular boundaries exhibited higher functional MPD, functional MNTD, and phylogenetic MNTD but reduced species richness. Moreover, wetlands located farther from major settlements and roads showed higher species richness, Shannon–Wiener diversity, and functional MPD. Notably, community assembly within these satellite wetlands was predominantly governed by stochastic processes. Based on these findings, management should prioritize the conservation of large satellite wetlands with diverse habitat structures to maintain habitat heterogeneity; enhance connectivity among wetlands to facilitate waterbird movement and dispersal; maintain moderate edge complexity to create varied microhabitats; and establish vegetation buffers near human infrastructure to reduce disturbance. Although limited to a single wintering season, the large number of surveyed sites provides robust spatial coverage, offering valuable insights for the conservation and management of fragmented wetlands.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: CL, GW. Data curation: MY, ZL. Formal analysis: MY, CL, WB. Investigation: MY, ZL. Writing – original draft: MY. Writing – review and editing: CL, GW, WB.

Author ORCIDs

Chunlin Li https://orcid.org/0000-0003-4161-9013
Willem F. de Boer https://orcid.org/0000-0003-3208-8521

Data availability

Data are contained in the supporting information or available from the authors upon reasonable request.

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Supplementary material 1

Waterbird species recorded in satellite wetlands around Chao Lake, middle and lower Yangtze River, China — scientific names and individual numbers

Authors: Mingyun Yuan, Guangyao Wang, Zhiru Lu, Chunlin Li, Willem F. de Boer

Data type: docx

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Link: https://doi.org/10.3897/natureconservation.63.177016.suppl1

Supplementary material 2

Functional traits (body mass, diet, foraging behavior, and habitat use) of waterbird species (scientific names) recorded in satellite wetlands around Chao Lake, in the middle and lower reaches of the Yangtze River, China

Authors: Mingyun Yuan, Guangyao Wang, Zhiru Lu, Chunlin Li, Willem F. de Boer

Data type: docx

Explanation note: Values of 1 indicate the presence of a given trait, and 0 indicates its absence. “Mass” represents the average adult body mass (g). “Invertebrates,” “Vertebrates,” and “Plants” denote primary diet categories; “Pursuit,” “Gleaning,” “Pouncing,” “Grazing,” “Digging,” and “Probing” describe foraging behaviors; and “Water,” “Mud,” and “Vegetation” indicate preferred foraging habitats.

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Link: https://doi.org/10.3897/natureconservation.63.177016.suppl2

Supplementary material 3

Functional dendrogram of waterbird species recorded in satellite wetlands around Chao Lake, in the middle and lower reaches of the Yangtze River, China

Authors: Mingyun Yuan, Guangyao Wang, Zhiru Lu, Chunlin Li, Willem F. de Boer

Data type: docx

Explanation note: The dendrogram illustrates functional relationships among waterbird species based on Gower distances of functional traits and UPGMA clustering. Branch lengths represent functional dissimilarities among species. This tree was used to quantify functional diversity and community structure.

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Link: https://doi.org/10.3897/natureconservation.63.177016.suppl3

Supplementary material 4

Phylogenetic tree of waterbird species recorded in satellite wetlands around Chao Lake, in the middle and lower reaches of the Yangtze River, China

Authors: Mingyun Yuan, Guangyao Wang, Zhiru Lu, Chunlin Li, Willem F. de Boer

Data type: docx

Explanation note: The phylogenetic tree shows evolutionary relationships among the waterbird species recorded in this study. Branch lengths are proportional to evolutionary divergence among species. This tree was used to calculate phylogenetic diversity and related community metrics.

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